



Ecological Changes in Miocene Mammalian Record Show Impact of Prolonged Climatic Forcing

Citation

Badgley, Catherine, John C. Barry, Michele E. Morgan, Sherry V. Nelson, Anna K. Behrensmeyer, Thure E. Cerling, David Pilbeam. 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences of the United States of America* 105(34): 12145-12149.

Published Version

doi:10.1073/pnas.0805592105

Permanent link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:3716602>

Terms of Use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at <http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA>

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. [Submit a story](#).

[Accessibility](#)

Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing

Catherine Badgley^{†*}, John C. Barry[‡], Michèle E. Morgan[‡], Sherry V. Nelson[§], Anna K. Behrensmeyer[¶], Thure E. Cerling^{*||}, and David Pilbeam[‡]

[†]Museum of Paleontology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109; [‡]Peabody Museum, Harvard University, Cambridge, MA 02138; [§]Anthropology Department, University of New Mexico, Albuquerque, NM 87131; [¶]Department of Paleobiology, Evolution of Terrestrial Ecosystems Program, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; and ^{||}Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112

Contributed by Thure E. Cerling, June 14, 2008 (sent for review January 27, 2008)

Geohistorical records reveal the long-term impacts of climate change on ecosystem structure. A 5-myrr record of mammalian faunas from floodplain ecosystems of South Asia shows substantial change in species richness and ecological structure in relation to vegetation change as documented by stable isotopes of C and O from paleosols. Between 8.5 and 6.0 Ma, C₄ savannah replaced C₃ forest and woodland. Isotopic historical trends for 27 mammalian herbivore species, in combination with ecomorphological data from teeth, show three patterns of response. Most forest frugivores and browsers maintained their dietary habits and disappeared. Other herbivores altered their dietary habits to include increasing amounts of C₄ plants and persisted for >1 myr during the vegetation transition. The few lineages that persisted through the vegetation transition show isotopic enrichment of $\delta^{13}\text{C}$ values over time. These results are evidence for long-term climatic forcing of vegetation structure and mammalian ecological diversity at the subcontinental scale.

faunal turnover | isotope ecology | mammals | paleocommunities | flood plain paleoecology

Long records of organisms and environments provide unique opportunities to evaluate the ecological and evolutionary responses of populations and ecological communities to environmental change over hundreds of thousands to millions of years. This historical perspective is essential for linking the dynamics of biotic change from ecological to evolutionary time scales and for understanding processes that transform ecosystems over geologic time. Here, we present evidence for the impact of local and regional climatic change on the species richness and trophic structure of Miocene mammals that inhabited sub-Himalayan alluvial plains. Stable isotopes of carbon and oxygen from paleosols document climate and vegetation, whereas carbon and oxygen isotopes from mammalian tooth enamel provide evidence for diets of herbivorous lineages. From 10.5 to 5.5 Ma, isotopic histories of species-level mammalian lineages reveal their responses to substantial changes in regional vegetation and climate.

The effects of climate on species' geographic ranges and the ecological structure of terrestrial biotas have been documented since the time of von Humboldt. For terrestrial mammals, climatic change has been linked to geographic-range shifts, fragmentation of populations, and selective filtering of populations over time and space—circumstances that can result in extinction or allopatric speciation as well as biotic turnover within ecosystems (1–5). Data from the fossil record do not, however, consistently match the predictions of this scenario of climate as a driver of mammalian evolution. This mechanism has been challenged when changes in taxonomic richness, origination rates, or extinction rates of regional or continental mammal faunas fail to track changes in the marine temperature record (as a proxy for global temperature) (6–8). On the other hand, notable changes in ecomorphological attributes, such as mean

cheek-tooth height (hypsodonty) of ungulate species from Neogene fossil assemblages, and in species richness and ecological structure of extant mammalian faunas can track climatic gradients over time (9) and space (10). These contrasting perspectives reflect the different spatial, temporal, and taxonomic scales of analysis. Resolving these divergent views requires long fossil records with high temporal and taxonomic resolution, as well as faunal and climatic data from the same geohistorical system. The Siwalik record of northern Pakistan is the longest, best documented sequence of terrestrial mammalian faunas of the last 20 myr (11). Multiple lines of geologic, isotopic, and ecomorphological evidence from this continuous record of floodplain ecosystems reveal the responses of mammalian herbivores to climatically mediated vegetation changes.

The Siwalik Record of Northern Pakistan. The Siwalik Group consists of alluvial sediments shed from the southern margin of the Himalayas over much of the Neogene. A well exposed sequence in the Potwar Plateau, south of Islamabad, Pakistan, has been studied by an interdisciplinary team of geologists and paleontologists for >30 years (11). In this area, Siwalik sediments > 4,000-m thick range from 18 to 1 Ma. Detailed lithostratigraphy and geochronology based on densely sampled magnetostratigraphy provide a stable temporal framework for fossil localities within an ancient flood basin tens of kilometers wide. Individual localities, spatially resolved to tens of meters squared, can be assigned with confidence to 100,000-yr intervals. Mammalian remains, documented by >50,000 catalogued specimens, dominate this fossil record. Major groups include common artiodactyls, perissodactyls, and rodents; uncommon primates, carnivores, and proboscideans; and rare creodonts, lagomorphs, aardvarks, and tree shrews (11). Surface collecting and screen washing have yielded substantial samples of large and small mammals, respectively. Although fossil plants are extremely rare from the Miocene deposits of the Potwar Plateau, stable isotopes from paleosol carbonates throughout the sequence provide evidence for vegetation composition on the flood plain. A large shift in carbon and oxygen isotope values during the late Miocene, initially documented in this Potwar Siwalik sequence, records changes in vegetation composition and structure linked to tectonic uplift and onset of the South Asian monsoon system (12–14). Isotopic analysis of mammalian tooth enamel independently documents changes in vegetation and precipitation

Author contributions: C.B., J.C.B., A.K.B., T.E.C., and D.P. designed research; C.B., M.E.M., S.V.N., and T.E.C. performed research; J.C.B. contributed new reagents/analytic tools; C.B., J.C.B., M.E.M., S.V.N., A.K.B., and T.E.C. analyzed data; and C.B. and A.K.B. wrote the paper.

The authors declare no conflict of interest.

*To whom correspondence may be addressed. Email: cbadgley@umich.edu or cerling@earth.utah.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0805592105/DCSupplemental.

© 2008 by The National Academy of Sciences of the USA

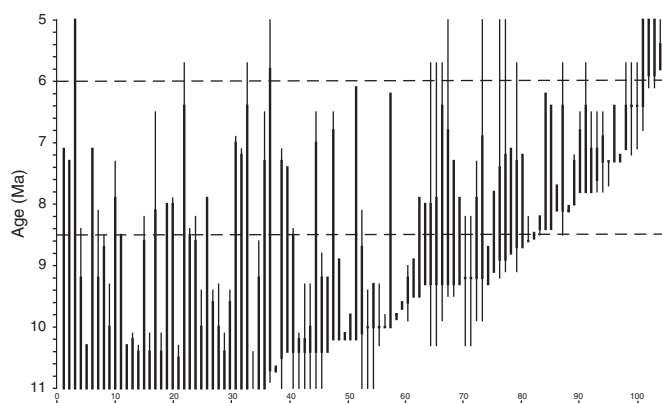


Fig. 1. Biostratigraphic ranges of 105 taxonomically resolved mammalian lineages from the late Miocene, Siwalik record of the Potwar Plateau. Most artiodactyls, perissodactyls, primates, and rodents are included. Most proboscideans, carnivores, and some small mammals are omitted. Dark lines connect observed first and last occurrences. Thin vertical lines represent 80% confidence intervals, calculated for the majority of lineages. Dashed horizontal lines bracket the interval of major environmental change. [Table S1](#) lists the lineages and age ranges that are the basis for this figure; updated from ref. 11.

sources and correlates well with the record from paleosol carbonates (15–17).

Our analysis focuses on the late Miocene interval from 10.5 to 5.5 Ma, represented by ≈ 550 fossil localities, $\approx 18,000$ vertebrate fossils, and ≈ 150 mammalian lineages from 13 mammalian orders. About two-thirds of these lineages are well resolved taxonomically, allowing us to evaluate residence times (local biostratigraphic ranges) and faunal turnover (appearances and disappearances of lineages) at the species level. The residence time of mammalian lineages in the Siwalik record varies from 0.1 myr (the maximum resolution of individual fossil localities) to several million years. Estimated biostratigraphic ranges, based on confidence intervals on observed ranges (11), establish the pattern of faunal turnover. Biogeographic data and phylogenetic analyses indicate that most newly appearing lineages did not have ancestors in older Siwalik faunas; thus, most first appearances represent immigration events. The inferred ranges of 105 lineages [Fig. 1 and [supporting information \(SI\) Table S1](#)] show that, over the late Miocene, standing richness of mammals decreased by more than half (from ≈ 50 to ≈ 20 taxonomically resolved species) and that turnover was continuous rather than pulsed. Rarefaction analysis validates the decline in species richness after standardization for interval sample size ([Fig. S1](#)). Dietary inferences for herbivores are based on general tooth morphology, tooth-crown height, dental microwear and mesowear, and stable carbon isotopes from enamel. In combination with intensive isotopic sampling, these data provide historical ecological profiles of individual lineages and herbivore trophic structure as flood plain vegetation changed from forest to grassland.

The Late Miocene Environmental Record. The paleoenvironmental record of this study, inferred from sedimentary facies, paleosol features, and stable isotopes of carbon and oxygen in pedogenic carbonates and mammal teeth, documents substrates, vegetation, and climate over 5 myr. The Miocene flood basin was traversed by large rivers—on the scale of major tributaries to the modern Indus and Ganges—and smaller flood plain channels (18–20). Paleosol sequences of variable maturity indicate the presence of forest, woodland, and grassland vegetation that was stable for decades to thousands of years (12, 14). Although shallow lacustrine sediments imply the presence of year-round water, the high frequency of pedogenic carbonate nodules signifies high seasonal evapotranspiration. C_3 plants dominated flood plain vegetation until the late Miocene, according to $\delta^{13}C$

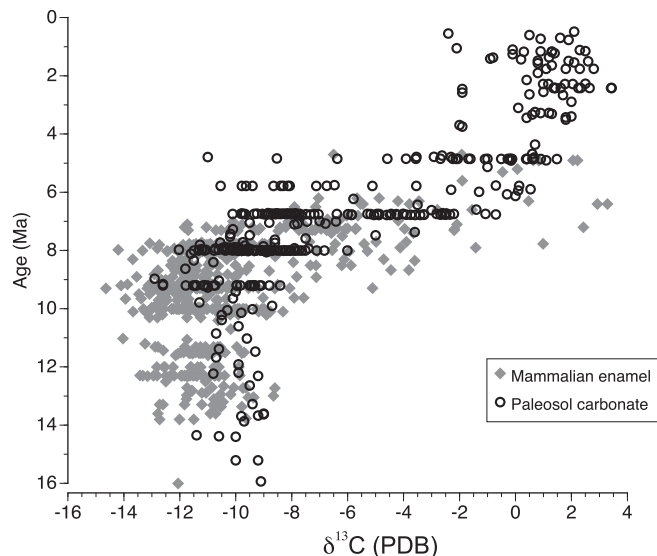


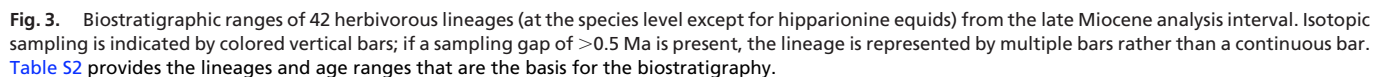
Fig. 2. Carbon isotope record from pedogenic carbonates (12, 14) and mammalian tooth enamel (15–17, this study) show a pronounced shift to lighter values starting ≈ 8.5 Ma. Over the well sampled interval from 9.5 to 7.0 Ma, mammalian $\delta^{13}C$ values vary more than do paleosol values, indicating that mammalian herbivores sampled a broader range of habitats than documented by the paleosol record. To facilitate comparison of paleosol and mammal $\delta^{13}C$ values with respect to vegetation, all paleosol values were adjusted by -1% because the fractionation values (vegetation to paleosol carbonate, vegetation to mammalian enamel) differ by this amount.

values of pedogenic carbonates (Fig. 2). Beginning ≈ 8.5 Ma, $\delta^{13}C$ values became increasingly enriched over time, reaching a new long-term average ≈ 6.0 Ma (12). Based on calibration of $\delta^{13}C$ values with modern vegetation, the C-isotopic shift signifies a transition from C_3 -dominated to C_4 -dominated vegetation. C_3 plants include trees, most shrubs, and cool-season grasses, whereas C_4 plants are primarily warm-season grasses (21).

Enrichment in $\delta^{18}O$ from pedogenic carbonates and mammalian teeth, beginning ≈ 9 Ma, signifies an increase in temperature, a decrease in precipitation, or a change in source of precipitation—any of which can be attributed to the onset of the Indian monsoon system (12). The prevalence of diverse crocodilians as well as the paleolatitude ($27\text{--}30^\circ N$) and low elevation imply that temperatures were well above freezing year round.

Isotopic historical trends were documented for mammalian herbivores and for individual lineages over the late Miocene interval of environmental change. Mammalian $\delta^{13}C$ values ($n = 570$) show a greater range of variation than do those from pedogenic carbonates (Fig. 2). This variation reflects dietary differences among individuals and species as mammals ranged across the sub-Himalayan flood basin and documents the presence of more closed and more open habitats than are represented by paleosol carbonates (17). Isotopic profiles and ecomorphological dietary information for individual lineages were evaluated in relation to appearances and disappearances of species to test the hypothesis that climatically driven vegetation change caused the observed faunal turnover.

Environmental Sorting of Species Through Time. A model of climatically driven sorting of species predicts that as vegetation habitats shrink, expand, or move across the landscape, herbivorous species reliant on particular plant resources will shift their geographic ranges to remain in their preferred habitats (2). In the Siwalik record, this scenario implies that species that relied on C_3 vegetation (forest fruit, browse) should disappear during the transition to C_4 vegetation (open grassland), resulting in local



Mixed feeders and grazing herbivores show quite a different pattern. Whereas 11 lineages disappeared between 8.5 and 6.0 Ma, 9 lineages appeared during this interval. Both the disappearing lineages and the appearing lineages include artiodactyls

9. Jernvall J, Fortelius M (2002) Common mammals drive evolutionary increase of hypsodonty in the Neogene. *Nature* 417:538–540.
10. Badgley C, Fox DL (2000) Ecological biogeography of North American mammals: Species density and ecological structure in relation to environmental gradients. *J Biogeogr* 27:1437–1467.
11. Barry JC, et al. (2002) Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology* 28:1–71.
12. Quade J, Cerling TE (1995) Expansion of C₄ grasses in the late Miocene of Northern Pakistan: Evidence from stable isotopes in paleosols. *Paleogeogr Paleoclimatol Paleoecol* 115:91–116.
13. Zhisheng A, Kutzbach JE, Prell WL, Porter SC (2001) Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan Plateau since Late Miocene times. *Nature* 411:62–66.
14. Behrensmeyer AK, et al. (2007) The structure and rate of late Miocene expansion of C₄ plants: Evidence from lateral variation in stable isotopes in paleosols of the Siwalik Group, northern Pakistan. *Geol Soc Am Bull* 119:1486–1505.
15. Morgan ME, Kingston JD, Marino BD (1994) Carbon isotopic evidence for the emergence of C₄ plants in the Neogene from Pakistan and Kenya. *Nature* 367:162–165.
16. Nelson SV (2003) *The Extinction of Sivapithecus* (Brill, Boston).
17. Nelson SV (2007) Isotopic reconstructions of habitat change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan. *Paleogeogr Paleoclimatol Paleoecol* 243:204–222.
18. Willis BJ (1993) Evolution of Miocene fluvial systems in the Himalayan foredeep through a two kilometer-thick succession in northern Pakistan. *Sediment Geol* 88:77–121.
19. Khan IA, Bridge JS, Kappelman J, Wilson R (1997) Evolution of Miocene fluvial environments, eastern Potwar Plateau, northern Pakistan. *Sedimentology* 44:221–251.
20. Zaleha MJ (1997) Intra- and extrabasinal controls on fluvial deposition in the Miocene Indo-Gangetic foreland, northern Pakistan. *Sedimentology* 44:369–390.
21. Ehleringer JR, Cerling TE, Helliker BR (1997) C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* 112:285–299.
22. Badgley C, Nelson S, Barry JC, Behrensmeyer AK, Cerling TE (2005) in *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution*, eds Lieberman DE, Smith RH, Kelley J (Brill, Boston), pp 29–46.
23. Belmaker M, Nelson S, Morgan ME, Barry J, Badgley C (2007) Mesowear analysis of ungulates in the middle to late Miocene of the Siwaliks, Pakistan: Dietary and paleo-environmental implications. *J Vertebr Paleontol* 27:46A.
24. Quade J, Solounias N, Cerling TE (1994) Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. *Paleogeogr Paleoclimatol Paleoecol* 108:41–53.
25. MacFadden BJ, Cerling TE, Harris JM, Prado J (1999) Ancient latitudinal gradients of C₃/C₄ grasses interpreted from stable isotopes of New World Pleistocene horse (*Equus*) teeth. *Glob Ecol Biogeogr* 8:137–149.
26. Flynn LJ, Jacobs LL (1982) Effects of changing environments on Siwalik rodent faunas of Northern Pakistan. *Paleogeogr Paleoclimatol Paleoecol* 38:129–138.
27. Nelson SV (2005) Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability. *Paleogeogr Paleoclimatol Paleoecol* 222:122–144.
28. Stott P (1990) Stability and stress in the savanna forests of mainland South-East Asia. *J Biogeogr* 17:373–383.
29. Mariotti A, Peterschmitt E (1994) Forest savanna ecotone dynamics in India as revealed by carbon isotope ratios of soil organic matter. *Oecologia* 97:475–480.
30. Yadava PS (1994) Savannas of North-East India. *J Biogeogr* 17:385–394.
31. van der Meulen AJ, Peláez-Campomanes, Levin SA (2005) Age structure, residents, and transients of Miocene rodent communities. *Am Nat* 165:108–125.
32. Cerling TE, Hart JA, Hart TB (2004) Stable isotope ecology in the Ituri Forest. *Oecologia* 13:5–12.
33. Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger J-J (1996) Isotopic biogeochemistry (13C, 18O) of mammalian enamel from African Pleistocene hominid sites. *Palaeos* 11:306–318.
34. Hoefs J (1997) *Stable Isotope Geochemistry* (Springer, Berlin).